

Epiphytic ferns and bryophytes of Tasmanian tree-ferns: A comparison of diversity and composition between two host species

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Abstract Ferns, bryophytes and lichens are the most diverse groups of plants in wet forests in south-eastern Australia. However, management of this diversity is limited by a lack of ecological knowledge of these groups and the difficulty in identifying species for non-experts. These problems may be alleviated by the identification and characterization of suitable proxies for this diversity. Epiphytic substrates are potential proxies. To evaluate the significance of some epiphytic substrates, fern and bryophyte assemblages on a common tree-fern species, *Dicksonia antarctica* (soft tree-fern), were compared with those on a rare species, *Cyathea cunninghamii* (slender tree-fern), in eastern Tasmania, Australia. A total of 97 fern and bryophyte species were recorded on *D. antarctica* from 120 trunks at 10 sites, and 64 species on *C. cunninghamii* from 39 trunks at four of these sites. The trunks of *C. cunninghamii* generally supported fewer species than *D. antarctica*, but two mosses (particularly *Hymenodon pilifer*) and one liverwort showed significant associations with this host. Several other bryophytes and epiphytic ferns showed an affinity for the trunks of *D. antarctica*. Species assemblages differed significantly between both sites and hosts, and the differences between hosts varied significantly among sites. The exceptionally high epiphytic diversity associated with *D. antarctica* suggests that it plays an important ecological role in Tasmanian forests. Evidently *C. cunninghamii* also supports a diverse suite of epiphytes, including at least one specialist species.

Key words: *Cyathea*, *Dicksonia*, liverworts, microhabitat, mosses, substrate preferences, tree-ferns.

INTRODUCTION

For management purposes and in most plant ecological studies, forest communities are typically defined using the composition of vascular plants in the canopy and under-storey vegetation. However a high portion of floristic diversity may exist at a much smaller scale, selecting and partitioning microhabitats according to substrate and microclimate. For example, bryophyte species often outnumber vascular species by a factor of four or five in the wet sclerophyll forests and cool temperate rainforests of the island of Tasmania, Australia (Jarman & Kantvilas 1994; Pharo & Blanks 2000). Also, an area of forest with a relatively homogeneous vascular flora is likely to contain a high degree of variation among bryophytes, lichens, fungi and ferns (often collectively referred to as cryptogams) (Jarman & Kantvilas 1994; Pharo & Blanks 2000).

The ecology and habitat requirements of cryptogam species are generally poorly understood, largely because field identification of many species is time consuming for experts, and impossible for non-experts. However, such knowledge is becoming important for

biodiversity-protection measures in forest management because cryptogams are abundant in wet forests exploited heavily for forestry. One option is to establish appropriate surrogates for cryptogam species composition and diversity. Substrate may be such a surrogate, and it continues to attract attention (Pharo & Blanks 2000; Pharo & Beattie 2002; Turner 2003). Epiphytic substrates often support diverse cryptogamic floras and provide unique microhabitats. The host species is one variable by which to characterize these microhabitats, and many tree species support distinctive epiphytic assemblages (Scott 1970; Slack 1976; Piippo 1982; Wolf 1994). It follows that hosts offering especially distinctive substrates are most likely to support distinctive epiphytic assemblages and specialist species. Tree-ferns, collectively, are such hosts.

Both tropical and temperate species of tree-fern provide favourable habitat for many epiphytic bryophyte and fern species (Pócs 1982; Hassall & Kirkpatrick 1985; Page & Brownsey 1986; Heatwole 1993; Medeiros *et al.* 1993; Ough & Murphy 1996; Moran *et al.* 2003). Tree-ferns do not undergo secondary growth, and therefore do not possess wood or bark. Instead, structural support is provided by a dense mass of intertwined adventitious roots that surround the stem (often referred to as a root mantle). The

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resulting 'trunk' (technically referred to as a caudex) of the fern offers a substrate quite distinct from seed-plant trunks. Texture and other trunk attributes also vary among tree-fern species.

Beever (1984) found that *Cyathea medullaris*, *Cyathea dealbata* and *Dicksonia squarrosa* in New Zealand each hosted a characteristic community of moss epiphytes. This was attributed to differences in the texture of the trunk. Similarly, Ashton (1986) suggested that the greater luxuriance of epiphytes on the trunks of *Dicksonia antarctica* than on *Cyathea australis* in wet eucalypt forest in Victoria, Australia, was due to the thicker, moister and more finely textured root mantle of *D. antarctica*. *Dicksonia antarctica* trunks had approximately twice the water-holding capacity of *C. australis* trunks (Ashton 1986).

Tasmania, situated at approximately 42 degrees south, is an island with a cool temperate climate and some large areas of tall wet forest that provide a multitude of humid microhabitats occupied by ferns and bryophytes. Epiphytic substrates, including trunks of two species of tree fern, are particularly well utilized in these forests.

Dicksonia antarctica (commonly known as soft tree-fern or man-fern) is the most abundant and widespread species of tree-fern in Tasmania. It dominates the understorey vegetation in many wet forests (Busby & Brown 1994; DPIWE 2001), and often extends into dry sclerophyll forest along streams. It ranges from sea level to approximately 900 m elevation (Garrett 1996).

Cyathea cunninghamii is present in Tasmania in very localized populations on the banks of low altitude streams (Garrett 1996), and often reaches heights of around 10 m. Its trunk is narrow (approx. 12–16 cm diameter), with visible, persistent frond bases, except in the lower few tens of centimetres of trunks of over 5 m in height, which become enveloped by a mantle of adventitious roots. This contrasts with the thick, soft and fibrous mat of all but the smallest *D. antarctica* trunks.

Two other species of tree-fern occur in Tasmania, *C. australis* and *Todea barbara*, as well as a putative hybrid between *C. australis* and *C. cunninghamii* (*C. X marcescens*) (McCarthy & Orchard 1998). These species appear to host relatively fewer epiphytes, perhaps because they occupy drier habitats.

This study assesses the diversity of bryophyte and fern epiphytes on tree-fern trunks in south-eastern Tasmania, to contribute to the evaluation of a substrate-as-surrogate approach to management of diversity. Specifically, it tests the hypotheses that the substrates provided by the tree-ferns *C. cunninghamii* and *D. antarctica* differ significantly in (i) epiphytic diversity (at the regional, site and trunk scales); (ii) relative frequencies of individual epiphytic species, and (iii) epiphytic species assemblages.

In addition to testing these hypotheses relating to host differences, the significance of site variation in influencing epiphytic assemblages on these tree-ferns was assessed so as to evaluate the appropriateness of host-presence as a surrogate for epiphytic species presence.

METHODS

Study sites

Floristic data on tree-fern epiphytes were collected from 10 sites in eastern and south-eastern Tasmania (Fig. 1; Table 1). *Dicksonia antarctica* was moderately to highly abundant at all sites. Four sites contained *Cyathea cunninghamii*. The choice of the remaining six sites aimed for an even geographical spread throughout the region. They were not restricted by vegetation type, except that they needed to contain *D. antarctica* more than 2 m tall. Sites with recent large-scale disturbance were avoided, although several sites were selectively logged perhaps 50–100 years ago. The size and shape of the areas in which sampling occurred were defined partly by the homogeneity of the forest in each location. The sampled trunks were generally spaced at less than 10 m apart and the study areas were no more than 100 m² in area, however, riparian sites were necessarily long and narrow so as to remain within the same forest-type.

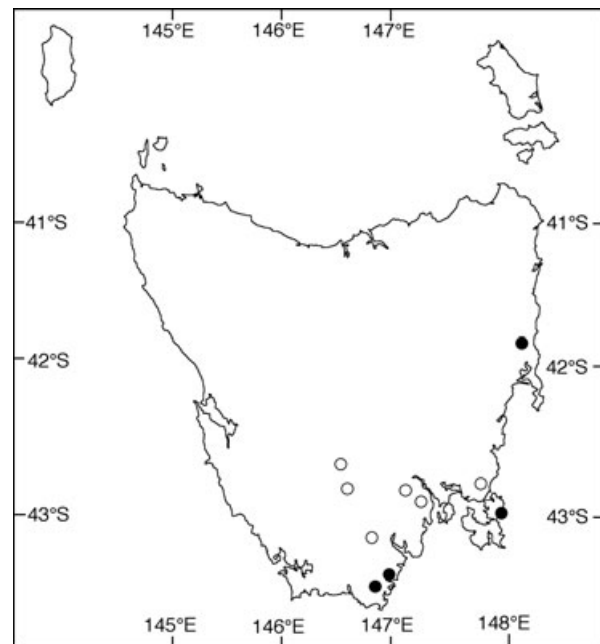


Fig. 1. Tasmania, showing the location of all field sites. Filled circles indicate the presence of *Cyathea cunninghamii*.

Table 1. Details of data collection sites. Annual precipitation was estimated using BIOCLIM (H. A. Nix, J. P. Busby, M. F. Hutchinson & J. P. McMahon unpubl. 1991; Hutchinson 1991). Vegetation types are based on Jackson (1999)

Location	Latitude	Longitude	Altitude (m)	Geology	Annual precipitation (mm)	Vegetation type	Topography
Florentine Valley	42°41'S	146°28'E	460	Ordovician limestone	1472	Thamnic rainforest	Mostly flat.
Big Tree Reserve, Styx Valley	42°49'S	146°39'E	320	Permian mudstone	1248	Mixed wet forest	Gentle north-facing slope
Arve River Picnic Reserve	43°10'S	146°49'E	150	Triassic sandstone	1329	Riparian mixed forest	East facing river bank
Hastings Caves State Reserve	43°23'S	146°51'E	120	Cambrian dolomite	1452	Mixed forest	Mostly flat, occasional undulations.
Dalco Creek, south of Dover	43°23'S	147°02'E	30	Jurassic dolerite	934	Riparian wet sclerophyll	Steep coastal gully, running East
Myrtle Forest Track, Wellington Range	42°52'S	147°09'E	580	Jurassic dolerite	1030	Riparian wet sclerophyll	Steep mountain gully, running North
Fern Glade Track, Mt Wellington	42°55'S	147°15'E	440	Permian mudstone	872	Riparian wet sclerophyll	Moderately sloping gully, running East
Sandspit River Forest Reserve	42°42'S	147°50'E	200	Jurassic dolerite	816	Relict rainforest (riparian)	Steep gully, running North
Western Creek, Tasman Peninsula National Park	43°00'S	147°57'E	40	Permian mudstone	852	Riparian, surrounded by wet sclerophyll	Steep coastal gully, running East
Lower Marsh Creek Forest Reserve	41°39'S	148°16'E	60	Devonian granite and metamorphics	798	Riparian, surrounded by dry sclerophyll	Very steep-sided gully, running East

Data collection

At each of the 10 study sites, 12 *D. antarctica* trunks were examined for epiphytes. Selection of trunks was random except that only live tree-ferns greater than two metres in height were chosen. Shorter ferns often have a 'skirt' of persistent dead fronds around the trunk, creating a dark and dry environment, which is unsuitable for epiphytes (Page & Brownsey 1986; N. R. Roberts pers. obs. 2002). Ferns leaning on other substrates were also avoided. At sites where *C. cunninghamii* was present, up to 12 trunks of this species (or as many as available and suitable) were also examined. For each trunk, all fern and bryophyte epiphytes that could be reached (i.e. below about 3 m), were recorded, plus any identifiable species that were beyond reach. Epiphyte loads above 3 m were usually very low.

Trunk water holding capacity was measured for five trunks of each host species at the Dalco Creek field site. Two samples of root-mantle, approximately 2 cm² in size, were taken from each fern (10 samples of each host species in total), from approximately 30 cm and 150 cm height on the trunk. The samples were immersed in tap water for 24 h followed by complete drainage for a further 20 h before being weighed. The samples were oven-dried at 60°C for 24 h, weighed again, and the water holding capacity was calculated as a percentage of the dry weight.

Species identification

All but three bryophyte and fern specimens were identified to species level, using Scott and Stone (1976) and Beever *et al.* (1992) for the mosses, Scott (1985) for hepatics and Duncan and Isaac (1986) for ferns. Revised taxonomic nomenclature was adopted, in accordance with Ratkovsky (1987), McCarthy and Orchard (1998) and Streimann and Klazenga (2002).

Some species identifications were tentative due the paucity of the material, while some thallose liverworts lacking reproductive structures could not be confidently identified. These specimens were excluded from comparative analysis. Fungi, algae, seed plants and categories of lichens (i.e. crustose, foliose, fruticose) were recorded but not identified beyond this taxonomic level. Voucher specimens of all identified species were deposited in the School of Plant Science, University of Tasmania.

Analysis

To test the significance of host-type and site as factors that may influence epiphytic species richness at the trunk level, per-trunk species richnesses were com-

pared with a two-way factorial analysis of variance, with host species and site as factors. This and other statistical analyses used the model fitting procedure of JMP 4 (SAS Institute Inc, Cary, NC, USA), except where noted. Because of uneven sample sizes, the effects of host species on whole site species richnesses were tested with paired *t*-tests after the data were rarefied (see Simberloff 1979) by repeated random subsampling to seven trunks of each host species at each site. Similarly, comparisons of total species richness across all sites were confounded by differences in sample size. To make a more valid comparison, the total diversity on *D. antarctica* was restricted to sites where *C. cunninghamii* was present, and then rarefied by repeated subsampling to the same number of trunks as *C. cunninghamii* at each site.

In order to detect patterns of similarity in the epiphyte assemblages between hosts and across sites, a robust ordination procedure, semi-strong hybrid multi-dimensional scaling (SSHMS), was employed. This used Bray Curtis distances of the presence/absence data for fern and bryophyte species on individual trunks, and was implemented with PATN (Belbin 1994). All *D. antarctica* and *C. cunninghamii* trunks were included.

The effects of host type (*C. cunninghamii* or *D. antarctica*), site (the sites where both hosts were present), and interaction between host and site on floristic composition were tested with two way factorial analysis of similarity based on Bray-Curtis distances as described above, using NPMANOVA (Anderson 2001; McArdle & Anderson 2001). Because this program requires balanced designs, two analyses were performed. One was based on a random subsample of seven trunks of each host species at the four sites where both species were present, and the other subsampled 10 trunks of each host species from the three sites where this was possible.

The association of individual epiphytic species with hosts was tested using logistic regression based on per-trunk presence or absence data, with host type and site as effects in the model.

The water holding capacities of the two species as percentages of dry weight were log transformed and compared with a factorial analysis of variance with species and height on the trunk as factors.

RESULTS

Ninety seven species of fern and bryophyte were recorded from the trunks of *D. antarctica*, and 64 from *Cyathea cunninghamii* (Table 2). A species list and frequencies of individual species have been published elsewhere (Roberts *et al.* 2003). Four of the species on *C. cunninghamii* were not recorded on *D. antarctica* trunks at any site, whereas 37 species were only

recorded on *D. antarctica*. On both host species ferns were the least species-rich epiphytic group, and mosses the most species-rich group (Table 2).

Lichens, especially crustose ones, were common on these tree-ferns, especially on *D. antarctica*. Seed plants, typically seedlings of tree species, were also quite common.

Relative species richness at two scales

Dicksonia antarctica supported significantly more species than *C. cunninghamii* at both the site and individual trunk scales (Figs 2,3). However for individual taxonomic groups this trend was only significant for hepatics and ferns at the scale of species per trunk.

Table 2. Species richness of epiphytic ferns and bryophytes on each host species across sites. Values in parenthesis are estimates of the number of species on *Dicksonia* when the sample size was reduced by rarefaction to the same as for *Cyathea*

	Dicksonia		Cyathea (n = 39)
	all sites (n = 120)	sites with Cyathea (n = 48)	
Ferns	16	15 (14.9)	12
Mosses	43	39 (36)	31
Hepatics	38	30 (28.5)	21
Total	97	84 (79.5)	64

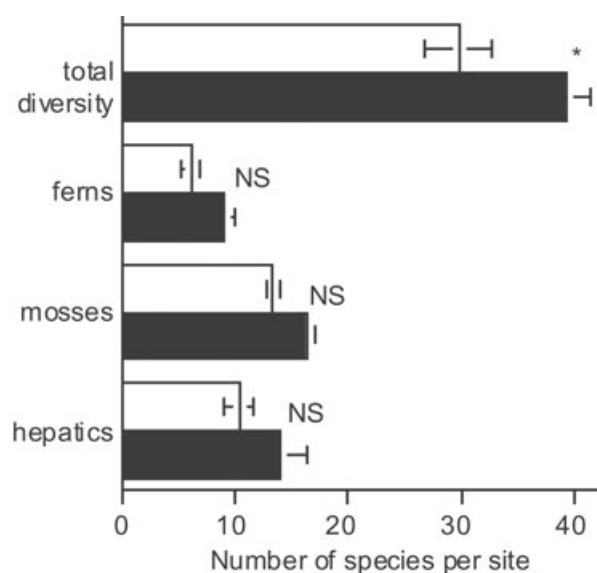


Fig. 2. Mean whole site species richnesses of epiphytes on *Cyathea* (open bars) and *Dicksonia* (closed bars), with standard errors, based on seven trunks per species per site. The significance of the difference between hosts (as estimated using paired *t*-tests) is indicated for each group of species (NS = $P > 0.05$; * $P < 0.05$; ** $P < 0.01$).

Species host preferences

Ten species showed significant host preferences (Fig. 4). Three ferns (*Hymenophyllum flabellatum*, *Hymenophyllum australe* and *Grammitis billardierei*), two mosses (*Rhizogonium novae-hollandiae* and *Plagiothecium lamprostachys*) and two hepatics (*Chiloscyphus echinellus* and *Tylimanthus diversifolius*) were recorded significantly more often on *D. antarctica* trunks than on *C. cunninghamii* trunks. In contrast, two mosses (*Hymenodon pilifer* and *Racopilum cuspidigerum* var. *convolutaceum*) and one liverwort (*Radula buccinifera*) were more common on *C. cunninghamii* than on *D. antarctica*. These trends were consistent across all four sites. *Hymenodon pilifer* was often very conspicuous on *C. cunninghamii* trunks, covering large areas of the trunk, reaching many metres of height and usually being by far the most abundant species on this host. Similarly, the *Hymenophyllum* species were often very conspicuous on *D. antarctica*, but not on *C. cunninghamii*.

Species assemblages

The epiphytic assemblages differed highly significantly ($P < 0.001$) between host species and among sites, both when three sites (with 10 replicates) and when four sites (with seven replicates) were analysed

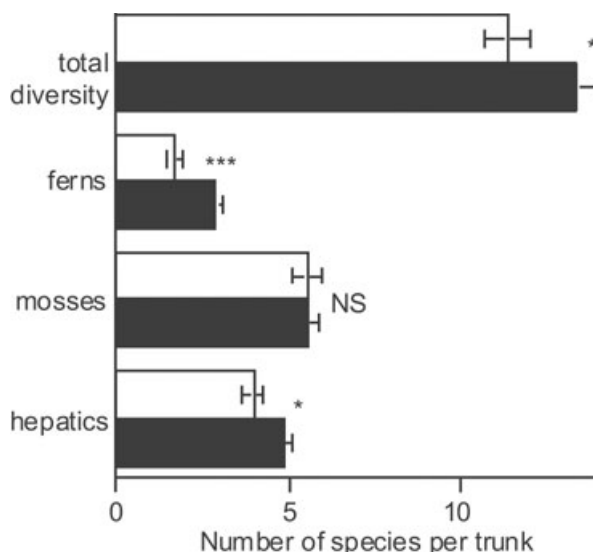


Fig. 3. Site averages of per trunk species richnesses of epiphytes on *Cyathea* (open bars) and *Dicksonia* (closed bars), with standard errors. The significance of the difference between hosts (as estimated using two way factorial analysis of variance) is indicated for each group of species (NS = $P > 0.05$; * $P < 0.05$; *** $P < 0.001$). All groups varied very significantly ($P < 0.001$) among sites, but site by host species interactions were not significant ($P > 0.05$).

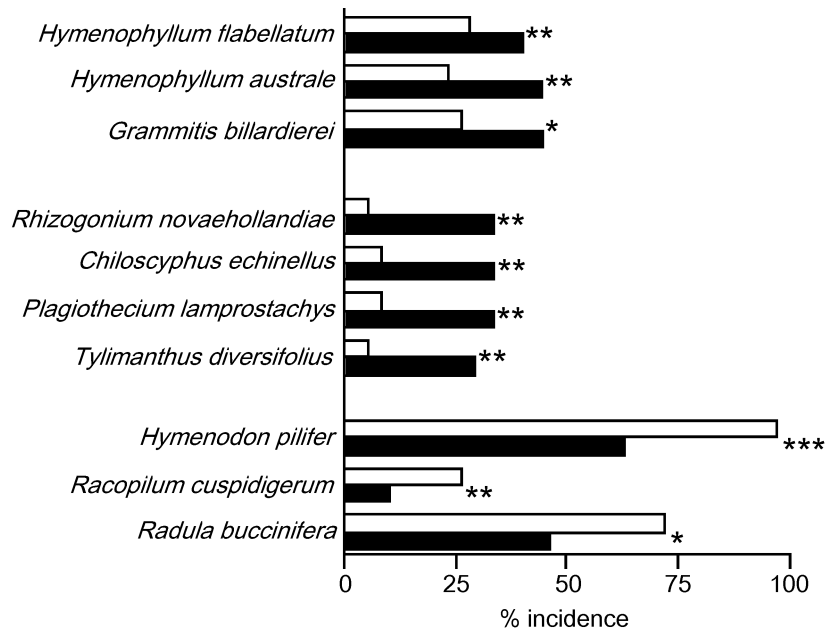


Fig. 4. Percentage incidence on host individuals across four sites of species showing a host preference for either *Cyathea* (open bars) or *Dicksonia* (closed bars). The significance of the difference (as estimated using logistic regression) is indicated for each species (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Most of these species also showed significant differences ($P < 0.05$) in abundance across sites.

Table 3. Non-parametric multivariate analysis of variance of floristic composition between host species and sites using 9999 random permutations. Two samples were analysed: one with 10 random trunks per host from three sites, and one with seven random trunks per host from four sites

Effect	Four site analysis		Three site analysis	
	F	P	F	P
site	5.3	≤ 0.0001	11.3	≤ 0.0001
host species	5.2	≤ 0.0001	8.1	≤ 0.0001
site*species	1.8	0.006	2.8	0.0001

(Table 3). Both analyses showed a significant interaction effect implying that the differences between host species were not the same at all sites. This effect was small compared to the host species and site effects (Table 3), but can be seen in Fig. 5. The host differences have different directions and sizes in the plot of vectors three and four (Fig. 5). Also the assemblages on *D. antarctica* at sites where *C. cunninghamii* occurs tend to be at one end of the spectrum for this host (Fig. 5). The assemblages on *C. cunninghamii* tend to extend further in this same direction.

The average water holding capacity of *D. antarctica* ($1168\% \pm 127\%$ [standard error] of oven-dried weight) was significantly ($P < 0.01$) greater than that of *C. cunninghamii* ($470\% \pm 56\%$). There was no significant difference in water holding capacity between the two heights (30 and 150 cm), and no significant

interaction effect ($P > 0.05$). Differences in water holding capacity between samples of the same host type appeared to correspond to differences in the texture of the adventitious roots.

DISCUSSION

The 81 bryophyte species on *Dicksonia antarctica* represent an exceptionally high species richness for a single host species. The 52 bryophyte species on *Cyathea cunninghamii* is less than would be found on a comparable sample of *D. antarctica* (approx. 64 species; Table 2), but this is still among the most species rich host-types known for bryophytic epiphytes. In comparison, Dalton (1998a) found 55 bryophyte species on the lower 2 m of 37 trunks of *Nothofagus cunninghamii* from 12 sites in western Tasmania, Mazimpaka and Lara (1995) identified 52 bryophytes on *Quercus pyrenaica* in Mediterranean deciduous woodland in Spain, and Franks and Bergstrom (2000) found 43 species on 25 trunks of *Nothofagus moorei* in south-eastern Queensland. Beever (1984) recorded 32 moss species on *Cyathea medullaris* in New Zealand compared to 43 species recorded in this study on *D. antarctica*. However, Beever (1984) sampled less than half as many trunks as this study and did not count hepatics. Thus, this New Zealand tree-fern may host at least as many bryophytes as the Tasmanian tree-ferns.

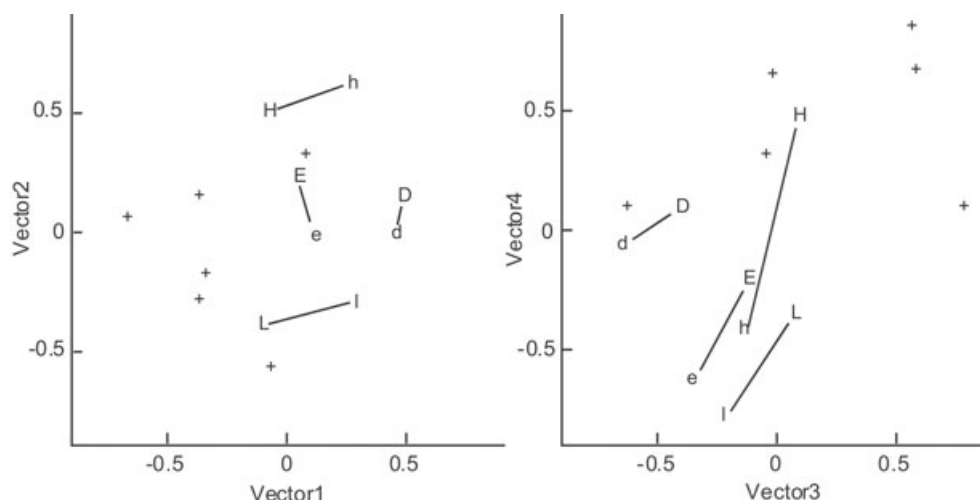


Fig. 5. Ordination plots based on a four dimensional semi strong hybrid multidimensional scaling of tree-fern trunk epiphyte assemblages. Capital and small case letters indicate the mean scores for assemblages on *Dicksonia* and *Cyathea* trunks, respectively. Assemblages on *Dicksonia* populations where *Cyathea* is absent are also shown (+). Standard errors for the site means on each vector ranged from 0.04 to 0.17, with no systematic pattern among groups.

Ferns are common and conspicuous epiphytes on *D. antarctica*, and to a lesser extent, *C. cunninghamii*. The relatively fewer fern species than bryophyte species does not imply that tree-ferns are poor hosts for ferns, but that bryophyte species vastly outnumber ferns in Tasmanian temperate forests (Dalton 1998b). In fact, epiphytic ferns are often abundant, and almost all of the typically epiphytic ferns occurring in Tasmania were on these tree-fern hosts. Several fern species show strong preferences for tree-fern trunks (e.g. Hymenophyllaceae and *Tmesipteris* spp.; Garrett 1996). Of these species, only *Tmesipteris obliqua* and *Hymenophyllum rarum* were not found on *C. cunninghamii* as well as *D. antarctica* in this study, possibly due only to insufficient sample size. Two species more typical of terrestrial environments (*Blechnum nudum* and *Polystichum proliferum*) were also found on *D. antarctica* trunks, suggesting the soft and fibrous root mantle of this species is suitable for the establishment of non-specialist species. Non-epiphytic seed plants (e.g. *Coprosma quadrifida*, *Pimelea drupacea*, *Pittosporum bicolor* and *Atherosperma moschatum*) were also frequently observed on this host.

Although not identified to species level, lichens were common and may contribute significantly to the epiphytic diversity on tree-ferns. Ford and Gibson (2000) found 25 lichen species growing on *D. antarctica* trunks in three rainforest sites in Victoria. They concluded that, although *D. antarctica* trunks generally make poorer hosts for lichens than other rainforest hosts such as *Nothofagus cunninghamii*, they nonetheless provide an important substrate, and are preferred by a few species.

Comparison of the two tree-fern hosts

At the trunk level, diversity of epiphytes, especially ferns, was significantly higher on *D. antarctica* than on *Cyathea cunninghamii*. Ferns are likely to be more dependent on their substrate for water and nutrients because they are endohydric, whereas bryophytes are primarily ectohydric in their water conduction. Substrate depth and water holding ability, both which apparently differ between the two tree-fern species, may therefore be important in defining habitat suitability for fern epiphytes.

At the site level, the difference between average diversity of the two hosts was even stronger, but the difference in diversity of fern epiphytes was not significant, indicating a high variation in fern species on *C. cunninghamii* from trunk to trunk within each site. These fern epiphytes are probably either *D. antarctica* specialists or generalist species, establishing only infrequently and opportunistically on *C. cunninghamii* trunks.

A few species were completely absent from one of the two hosts, but it was unclear whether these species were displaying actual host preference because they were also rare on the other host. Some of the more common species showed relative preferences for one host over the other, despite not being exclusive to this host. The three fern species that had significant preferences (*Hymenophyllum flabellatum*, *Hymenophyllum australe* and *Grammitis billardieri*) favoured *D. antarctica* trunks (Fig. 4), which was consistent with the higher fern diversity per trunk on this host. However, despite the greater bryophyte diversity on

D. antarctica, two mosses and one hepatic displayed significant host preferences for *C. cunninghamii*. In fact, the strongest epiphyte-host association in this study was that of the moss *Hymenodon pilifer* for *C. cunninghamii*.

Dicksonia antarctica and *C. cunninghamii* supported significantly different epiphytic assemblages to each other within sites, and furthermore, assemblages differed significantly among sites for both hosts (Table 3). Thus host-type may not have been the most important determinant of epiphytic habitat. In both cases the factors relevant in defining habitat were not obvious. Substrate features seemed the most apparent difference between the hosts, whereas meso- and micro- climatic differences were likely to account for much of the variation between sites. Disturbance history, the availability of other substrates, animal interactions, and dispersal limitations could also have affected the distribution of species. Data are scarce or lacking concerning the influence of these site factors on epiphyte assemblages in Australia. However, an exception is Turner (2003) who found, in addition to host differences, that the bryophyte assemblages of some substrates differed significantly among forests of different ages in Tasmania.

The presence of a highly significant interaction effect between host species and site (Table 3, most apparent in plot of vectors 3 and 4 in Fig. 5) implied that the differences between hosts were site dependent. The assemblages on *D. antarctica* at sites where *C. cunninghamii* was also present were loosely clustered at one side of the ordination space, and assemblages on *C. cunninghamii* trunks tended to be located even further in that direction. This trend may reflect an environmental vector across the ordination space. This may be moisture availability, because the sites containing *C. cunninghamii* tended to be in lower rainfall areas than sites where *D. antarctica* occurred alone. Also the trunks of *C. cunninghamii* have a much lower water holding capacity than *D. antarctica*, apparently due to a less developed, coarser and less fibrous root-mantle.

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